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Abstract: Grizzly bears (*Ursus arctos*) in the Greater Yellowstone Ecosystem (GYE) are opportunistic omnivores that eat a great diversity of plant and animal species. Changes in climate may affect regional vegetation, hydrology, insects, and fire regimes, likely influencing the abundance, range, and elevational distribution of the plants and animals consumed by GYE grizzly bears. Determining the dietary breadth of grizzly bears is important to document future changes in food resources and how those changes may affect the nutritional ecology of grizzlies. However, no synthesis exists of all foods consumed by grizzly bears in the GYE. We conducted a review of available literature and compiled a list of species consumed by grizzly bears in the GYE. We documented ≥266 species within 200 genera from 4 kingdoms, including 175 plant, 37 invertebrate, 34 mammal, 7 fungi, 7 bird, 4 fish, 1 amphibian, and 1 algae species as well as 1 soil type consumed by grizzly bears. The average energy values of the ungulates (6.8 kcal/g), trout (*Oncorhynchus* spp., 6.1 kcal/g), and small mammals (4.5 kcal/g) eaten by grizzlies were higher than those of the plants (3.0 kcal/g) and invertebrates (2.7 kcal/g) they consumed. The most frequently detected diet items were graminoids, ants (Formicidae), whitebark pine seeds (*Pinus albicaulis*), clover (*Trifolium* spp.), and dandelion (*Taraxacum* spp.). The most consistently used foods on a temporal basis were graminoids, ants, whitebark pine seeds, clover, elk (*Cervus elaphus*), thistle (*Cirsium* spp.), and horsetail (*Equisetum* spp.). Historically, garbage was a significant diet item for grizzlies until refuse dumps were closed. Use of forbs increased after garbage was no longer readily available. The list of foods we compiled will help managers of grizzly bears and their habitat document future changes in grizzly bear food habits and how bears respond to changing food resources.

Key words: climate change, diet, food habits, grizzly bear, nutritional ecology, *Ursus arctos*, Yellowstone Ecosystem

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Introduction

Grizzly bears (*Ursus arctos*) evolved with an opportunistic, generalist omnivore foraging strategy that allows them to occupy a wide array of the world's biomes (Bojarska and Selva 2011, Schwartz et al. 2013). This dietary plasticity at least partially explains why brown bears are the most widely distributed bear species in the world. In North America, grizzly bears once occupied many different habitats ranging from Arctic tundra in northern Alaska to arid regions of the southwestern United States and Mexico, and from the Great Plains west to the Pacific coast states of Washington, Oregon, and California, USA (Schwartz et al. 2003). After European settlement of North America, grizzly bear numbers and range south of Canada were significantly reduced (Mattson et al. 1995). Grizzly bear habitat was eliminated by construction of cities,

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towns, and homesteads (Haroldson et al. 2008). Habitat was altered by livestock grazing, agriculture, logging, and mining. Populations of important bear foods such as salmon (*Oncorhynchus* spp.), bison (*Bison bison*), and elk (*Cervus elaphus*) were greatly reduced by dam building, market hunting, and competition from livestock. In addition, grizzly bears were poisoned, trapped, and shot to reduce depredation on domestic cattle, sheep, swine, and poultry (Storer and Tevis 1955, Brown 1985, Gill 2010).

By the 1920s and 1930s, grizzly bears in the contiguous United States had been reduced to <2% of their historical range (Mattson et al. 1995, Servheen 1999) and by the 1950s had been extirpated from most areas outside of Alaska and Canada (Cowan et al. 1974). In the lower 48 states, grizzly bears still persisted in Washington, Idaho, and Montana adjacent to the Canadian border, and in 3 small isolated populations further south (Cowan et al. 1974). The 3 isolated populations included the mountains of Chihuahua, Mexico (the Sierra del Nido and possibly the Sierra Madre); the San Juan Mountains of southwestern Colorado; and the Yellowstone Plateau region of Wyoming, Montana, and Idaho, often referred to as the Greater Yellowstone Ecosystem (GYE). Because of its large size, remoteness, and the protections afforded by national park, national forest, and national wildlife refuge status over a large portion of the area, the GYE grizzly bear population was the only one of these 3 isolated populations that persisted in viable numbers after the 1960s (Cowan et al. 1974). In 1975, after high mortality associated with closing of garbage dumps inside and outside of Yellowstone National Park, grizzly bears in the GYE were listed as a Threatened Species under the Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 1993).

Even with Threatened Species protections, human activities will likely continue to affect the GYE grizzly bear population through influences on climate (Schwartz et al. 2013) and the introduction of exotic plants, animals, and diseases (Reinhart et al. 2001). Changes in climate may affect regional vegetation, hydrology, insects, and fire regimes (Schwartz et al. 2013), likely influencing the abundance, range, and elevational distribution of the plants and animals consumed by grizzly bears. Because of changing climate and the introduction of exotic species, some current grizzly bear foods may increase, others may decrease, and some may be locally extirpated. Changing climate may also allow plant species not native to the GYE to occupy the region. Some of these encroaching species may be beneficial food items for grizzly bears (e.g., *Quercus gambelii;* Rehfeldt et al. 2006), while others may not. Additionally, some exotic plant and animal species may obtain a competitive advantage for space and resources over native species. Successful long-term management and conservation of grizzly bears in the GYE will thus depend on a thorough understanding of current grizzly bear diets and nutritional ecology (Schwartz et al. 2013).

Plant, animal, and fungi foods consumed by grizzly bears in the GYE have been documented in many technical articles, books, Ph.D. dissertations, M.S. theses, and state and federal agency administrative reports. However, no single source has compiled all foods consumed by grizzly bears in the GYE. We conducted a literature review and compiled a list of all reported plant, fungi, vertebrate, and invertebrate species consumed by grizzly bears in the GYE. We also report on the nutritional and energetic value of bear food items and assess trends in use of some major bear foods over time. Our goal was to develop a resource for managers of grizzly bears and their habitat to document future changes in bear foods and potential impacts of these changes on the nutritional ecology of GYE grizzly bears.

Study area

Our study area encompassed the GYE, which includes 3 national park units (Yellowstone, Grand Teton, and John D. Rockefeller, Jr. Memorial Parkway), all or portions of 6 adjacent national forests (Beaverhead–Deer Lodge, Bridger–Teton, Caribou–Targhee, Custer, Gallatin, and Shoshone), 3 national wildlife refuges (National Elk Refuge, Red Rock Lakes, and Grays Lake), public lands administered by the Bureau of Land Management and Bureau of Reclamation, plus state and private lands in portions of Wyoming, Montana, and Idaho. Much of the habitat in the GYE is relatively pristine, undeveloped public land. Throughout the past 2 decades grizzly bears in the GYE have been expanding their range (Schwartz et al. 2002, 2006) and currently occupy >50,000 km^2 (Bjornlie et al. 2014). A primary component of occupied grizzly bear range within the GYE is the 23,833-km^2 Yellowstone Grizzly Bear Recovery Zone (USFWS 1993).

The GYE is geographically defined as the Yellowstone Plateau and 14 surrounding mountain ranges above 1,500 m (Anderson 1991, Patten 1991). Long, cold winters and short, cool summers characterize the climate of the Yellowstone Plateau. Areas below 1,900 m feature foothill grasslands or shrub steppes. With increasing moisture, open stands of Rocky Mountain juniper (*Juniperus scopulorum*), limber pine (*Pinus flexilis*), and Douglas-fir (*Pseudotsuga menziesii*) occur. Douglas-fir forms the lowest elevation forest community at around 1,900–2,200 m (Patten 1963, Waddington and Wright 1974, Romme and Turner 1991). Lodgepole pine (*Pinus contorta*) dominates the extensive Yellowstone Plateau at mid-elevations (2,400 m), where poor rhyolite-based soils are prevalent (Despain 1990). With increasing elevation, Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests dominate. Engelmann spruce and whitebark pine (*Pinus albicaulis*) form the upper tree line around 2,900 m (Patten 1963, Waddington and Wright 1974, Despain 1990). Alpine tundra occurs at elevations from 3,000 m to the highest reaches of all major mountain ranges (Despain 1990).

Methods

Literature review

The dietary breadth of GYE grizzly bears was determined by reviewing 49 published papers, 17 books, 4 Ph.D. dissertations, 11 M.S. theses, and 97 state and federal agency administrative reports that documented grizzly bear food habits in the GYE during the 123-year period from 1891 through 2013. Documentation of grizzly bear foods from 1891 through 1942 were from anecdotal descriptions written by early GYE naturalists. Documentation of grizzly food habits from 1943 through 2013 were from more rigorous scientific studies incorporating direct observations of grizzly bear feeding activities, field examination of grizzly bear feeding sites, and laboratory analyses of grizzly bear scats. From these sources we compiled a list of species consumed by GYE grizzly bears. We arranged the list of grizzly bear foods first by the 6 biological kingdoms (Plantae, Animalia, Fungi, Protista, Archaea, Bacteria) and then alphabetically within those groups by phylum (invertebrates only), family, genus, and species. Family, genus, and species were not always reported for invertebrates. Plant nomenclature followed U.S. Department of Agriculture-Natural Resources Conservation Service [USDA-NRCS] 2012). Large mammal and small mammal nomenclature followed Feldhamer et al. (2003) and Streubel (1989), respectively. Common names used for plants followed Whipple (2011) and those not listed in Whipple (2011) followed Kershaw et al. (1998).

When available from the literature, we report the gross energy and nutritive value of diet items consumed by grizzly bears. Gross energy values for diet items are reported on a dry weight basis as kilocalories per gram (kcal/g). When available, we also report the nutritive values of foods consumed, including the percentage composition of protein, fat, and carbohydrate of the diet item.

Diet items in bear scats

Frequency of occurrence. We compiled scat composition data from all GYE grizzly bear studies where scat data were reported. These studies included diet items from 11,478 scats collected during 37 years of the 67-year period from 1943 through 2009. Scat composition data reported by Craighead et al. (1995) for the years 1968 through 1971 were combined when reported and therefore represented an average for that time period. For comparison, we calculated percent frequency of occurrence for each specific diet item. The percent frequency of occurrence equaled the total number of times a specific food item appeared in scats of the sample, divided by the total number of scats collected (n = 11,478). Greater values implied greater number of times a food item was consumed, but did not reflect total volume consumed. In grouped data presentations, food items are presented in rank order from highest to lowest percent frequency of occurrence.

Diet item stability. As a measure of temporal diet item stability, we calculated the percent of sample years each diet item was detected in scats. Our measure of diet item stability was calculated as the total number of years a diet item was detected in scats, divided by the total number of years scats were collected. Greater values implied greater temporal stability in use of food items, whereas smaller values implied greater year-to-year fluctuations in use. Because the 1968–1971 data collected by Craighead et al. (1995) were not reported by individual year, we censored scat composition data from that time period for calculation of diet item stability. As in the percent frequency of occurrence calculations, the diet item stability calculations did not reflect total volume consumed.

Shifts in major food groups. To determine whether shifts in grizzly bear diet had occurred in the GYE between 1943 and 2009, we calculated the percent frequency of occurrence of major food groups detected in bear scats by time period. We defined major food groups as follows: graminoids, forbs, whitebark pine seeds, trout, berries, mammals, ants, mushrooms, and garbage. We grouped annual data on diet item composition into 6 time periods: 1943, 1968–1971, 1973–1979, 1980–1989, 1990–1998, and 2004–2009. Scat composition data reported by Craighead et al. (1995) for 1968–1971 were combined when reported so we maintained that grouping.

Results

Diet items

We documented 266 species in 200 genera from 4 kingdoms (Plantae, Animalia, Fungi, and Protista), plus a soil type (geothermal), consumed by GYE grizzly bears (Table 1). Grizzly bears consumed ≥162 plant species (149 native, 13 non-native) including forbs (n = 85), graminoids (n = 31), shrubs (n = 31), trees (i.e., cambium, catkins, and nuts; n = 7), aquatic plants (n = 4), and ferns and fern allies (n = 4; Table 1; Table S1). Seven species of mushrooms were consumed including gilled (n = 3) and non-gilled (n = 4). We also documented bears feeding on ≥26 mammal, 4 fish, 3 bird, and 1 amphibian species, although additional bird and mammal species are undoubtedly consumed opportunistically. Grizzly bears also consumed ≥36 species of invertebrates including insects (n = 33), segmented worms (n = 1), mollusks (n = 1), and spiders (n = 1). We documented consumption of 1 algae and 1 soil type (geophagy). Additionally, grizzly bears consumed ≥26 species of domestic plants and animals, including cultivated agricultural, garden, and ornamental plants (n = 13), domestic livestock (n = 7), domestic poultry (n = 4), domestic dogs (n = 1), and domestic honey bees (n = 1).

The reported gross energy values (kcal/g) of specific foods consumed by grizzly bears in the GYE ranged from 1.91 kcal/g for the roots of green false-hellebore (*Veratrum viride*) to 7.91 kcal/g for army cutworm moths (*Euxoa auxiliaris;* Table S2). Foods with the greatest reported gross caloric values were army cutworm moths, ungulates (6.80 kcal/g), cutthroat trout (*Oncorhynchus clarkii;* 6.10 kcal/g), clover (*Trifolium* spp.; 4.83 kcal/g), small mammals (4.50 kcal/g), and seeds of whitebark pine (3.99 kcal/g). Berries had an average gross caloric value of 3.24 kcal/g, forbs 2.88 kcal/g, and grasses and sedges 2.52 kcal/g.

Table 1. Number of species in different kingdoms consumed by grizzly bears in the Greater Yellowstone Ecosystem, 1891–2013.

Kingdom	Category	No. of species
Plantae	Aquatics	4
	Ferns and fern allies	4
	Forbs	85
	Graminoids	31
	Shrubs	31
	Trees	7
Fungi	Gilled mushrooms	3
	Non-gilled mushrooms	4
Animalia	Vertebrates	
	Amphibians	1
	Birds	3
	Fish	4
	Mammals	26
	Invertebrates	
	Insects	33
	Mollusks	1
	Segmented worms	1
	Spiders	1
Protista	Algae	1
Anthropogenic Foods	Cultivated plants	13
	Domestic dogs	1
	Domestic livestock	7
	Domestic poultry	4
	Domestic insects	1
Total		266[a]

[a]In addition to the 266 species consumed, grizzly bears were also documented consuming geothermal soil.

Plant foods with the highest protein content were the pre-flowering foliage of springbeauty (*Claytonia lanceolata;* 39.0%), flowering heads of cow-parsnip (*Heracleum sphondylium;* 26.3%), newly emerging leaves of western meadow-rue (*Thalictrum occidentale;* 24.4%), foliage of clover (23.1%), and the flowering heads of beargrass (*Xerophyllum tenax*; 21.1%).

Highest fat content (ether extract) of plant foods were from the seeds of whitebark pine (30.5%); the berries of red-osier dogwood (*Cornus sericea;* 20.2%), red baneberry (*Actaea rubra;* 19.3%), red elderberry (*Sambucus racemosa;* 19.1%), and creeping juniper (*Juniperus horizontalis;* 18.6%); and the seed pods of beargrass (15.6%).

Carbohydrates (nitrogen-free extracts) were highest in the bulbs of oniongrass (*Melica spectabilis;*

88.8%), tubers of yampa (*Perideridia gairdneri borealis;* 87.6%), bulbs of glacier lily (*Erythronium grandiflorum;* 81.9%), roots of biscuitroot (*Lomatium* spp.; 77.6%), and corms of springbeauty (77.1%). Berry species also had a high average carbohydrate value (55.0%).

Frequency of occurrence in scats

Based on 11,478 scats collected during 37 years from 1943 to 2009, the most frequently detected food items consisted of 39 taxonomically distinguishable foods (Table 2). The most frequently occurring foods were graminoids (primarily bluegrass [*Poa pratensis*], sedges [*Carex* spp.], and brome grass [*Bromus* spp.]; 58.7%), ants (primarily *Camponotus* spp. and *Formica* spp.; 15.8%), whitebark pine seeds (15.4%), clover (primarily *Trifolium repens;* 11.9%), and dandelion (primarily *Taraxacum officinale;* 10.9%). Other frequently detected diet items included elk (8.3%), thistle (primarily *Cirsium foliosum* and *C. scariosum;* 6.9%), horsetail (primarily *Equisetum arvense;* 5.6%), yampa roots (4.9%), vaccinium berries (primarily *Vaccinium scoparium* and *V. membranaceum;* 4.9%), cutthroat trout (4.4%), biscuitroot (primarily *Lomatium cous* and *L. triternatum;* 4.0%), springbeauty (2.9%), bison (2.8%), and fireweed (*Chamerion angustifolium;* 2.7%). Mushrooms (primarily false truffles, *Rhizopogon* spp.), oniongrass bulbs, bistort (primarily *Bistorta bistortoides*), cow-parsnip, strawberry (primarily 2 species [*Fragaria virginiana* and *F. vesca*]), pocket gophers (*Thomomys talpoides*), deer (*Odocoileus* spp., primarily mule deer [*O. hemionus*]), army cutworm moths, voles (primarily 2 species—montane vole [*Microtus montanus*] and meadow vole [*M. pennsylvanicus*]), buffaloberry (*Shepherdia canadensis*), yellow salsify (*Tragopogon dubius*), sweet-cicely (primarily 2 species [*Osmorhiza berteroi* and *O. occidentalis*]), gooseberry (primarily *Ribes cereum*), fern-leaf licoriceroot (*Ligusticum filicinum*), and moose (*Alces alces*) were detected in from 0.5% to 2% of scats. An additional 127 species from 121 genera were detected in <0.5% of bear scats.

Table 2. Percent frequency of occurrence of the diet items most often detected in 11,478 grizzly bear scats collected in the Greater Yellowstone Ecosystem (GYE) during 37 years between 1943 and 2009.

Food item[a]	Frequency of occurrence in scats[b] Number	Percent
Graminoids (primarily 3 species)[c]	6,732	58.7
Ants (primarily from 2 genera)[d]	1,810	15.8
Whitebark pine	1,769	15.4
Clover	1,371	11.9
Dandelion	1,249	10.9
Elk	957	8.3
Thistle (primarily 2 species)	795	6.9
Horsetail	645	5.6
Yampa	560	4.9
Vaccinium berries (primarily 2 species)	557	4.9
Cutthroat trout	507	4.4
Biscuitroot (primarily 2 species)	460	4.0
Spring beauty	338	2.9
Bison	326	2.8
Fireweed	312	2.7
Mushrooms	211	1.8
Oniongrass	181	1.6
Bistort	152	1.3
Cow-parsnip	133	1.2
Strawberry (2 species)	131	1.1
Pocket gopher	98	0.9
Deer (primarily mule deer)	96	0.8
Army cutworm moths	89	0.8
Voles (primarily 2 species)	89	0.8
Buffalo berry	84	0.7
Yellow salsify	81	0.7
Sweet-cicely (2 species)	74	0.6
Gooseberry	68	0.6
Licoriceroot	68	0.6
Moose	56	0.5

[a]An additional 127 species were identified in bear scats but were detected in <0.5% of the total scats collected.
[b]Based on 37 yr for which scat composition data for the GYE were available in the literature.
[c]A total of 31 species of graminoids were consumed by grizzly bears, but individual species could not always be identified in scats.
[d]A total of 24 species of ants were consumed by grizzly bears, but individual species could not always be identified in scats.

Diet item stability

Based on scats collected during 33 years between 1943 and 2009, graminoids, ants, and whitebark pine seeds were each documented during all years that scats were collected (Table 3). Clover (97%), elk (94%), thistle (94%), horsetail (94%), biscuitroot (88%), dandelion (88%), vaccinium berries (85%), yampa (79%), oniongrass (76%), bison (73%), and fireweed (73%) were detected most years. Springbeauty (64%), cutthroat trout (58%), mushrooms (58%), deer (58%), and buffalo berry (55%) were detected over half of the years scats were collected. Cow-parsnip (48%), pocket gophers (48%), strawberry (45%), moose (45%), bistort (42%), and voles (42%) were detected nearly half of the years sampled. Gooseberry (39%), sweet-cicely (30%), yellow salsify (21%), and fern-leaf licoriceroot (21%) were consumed more opportunistically, showing

Table 3. Annual diet-item stability of the most frequently detected foods identified in grizzly bear scats collected in the Greater Yellowstone Ecosystem (GYE) during 33 years between 1943 and 2009.

	Years detected in scats[a]	
Food item	Number	Percent
Graminoids	33	100
Ants	33	100
Whitebark pine	33	100
Clover	32	97
Elk	31	94
Thistle	31	94
Horsetail	31	94
Biscuitroot	29	88
Dandelion	29	88
Vaccinium berries	28	85
Yampa	26	79
Oniongrass	25	76
Bison	24	73
Fireweed	24	73
Springbeauty	21	64
Cutthroat trout	19	58
Mushrooms	19	58
Deer	19	58
Buffalo berry	18	55
Cow-parsnip	16	48
Pocket gopher	16	48
Strawberry	15	45
Moose	15	45
Bistort	14	42
Voles	14	42
Gooseberry	13	39
Sweet-cicely	10	30
Yellow salsify	7	21
Licoriceroot	7	21
Army cutworm moths	3[b]	9

[a]Based on 33 yr for which scat composition data for individual years were available in the literature for the GYE.

[b]Due to the remoteness and inaccessibility of army cutworm moth aggregations sites, they are substantially under-represented in the scat sample. Direct observation of grizzly bear feeding activity at army cutworm moth sites from fixed-wing aircraft suggests that moths are likely used by grizzly bears nearly every year (see Bjornlie and Haroldson 2013).

periodic years of high use, separated by years with no use.

Shifts in major food groups

Based on scat composition data, a major diet shift occurred in the GYE in the early 1970s. Percent frequency of occurrence of garbage detected in scats increased from 18% in 1943 to 36% during 1968–1971 (Fig. 1). The percent frequency of occurrence then decreased to 2% of scats from 1973 through 1989, and <1% among scats collected in the 1990s. Garbage was not detected in scats after the year 2000. Scat composition data indicate that grizzly bears consumed more forbs as use of garbage decreased. In addition, a minor dietary shift in detection of cutthroat trout was observed. Cutthroat trout were not detected in scats collected from 1943 through 1971, but were detected in 5% of scats during 1973–1979, 7% of scats in the 1980s, and 3% of scats in the 1990s. Cutthroat trout were not detected in scats after the year 2000. Although fish are generally underrepresented in scats because of their high digestibility (Hewitt 1989, Pritchard and Robbins 1990, Craighead et al. 1995), feeding-site examinations and elemental analysis of hair also indicate that cutthroat trout were not a significant diet item for GYE grizzly bears after the year 2000 (Fortin et al. 2013, Teisberg et al. 2014).

Discussion

Anecdotal descriptions from 1891 through 1942 and extensive food-habits studies conducted from 1943 through 2013 indicate that GYE grizzly bears consumed numerous species, which varied in their energetic value, abundance, and availability both spatially and temporally. Our review of literature involved studies that used direct observation of grizzly bear feeding activities, examination of grizzly bear feeding sites, and analysis of grizzly bear scat composition. These studies indicated that grizzly bears in the GYE consumed ≥266 species from 200 genera in 4 kingdoms, plus 1 soil type. Some species detected in bear scats may represent exploratory consumption (sampling) while bears searched for potential new foods. Several species detected in scats (including algae [Protista], larkspur [*Delphinium* spp.], hawksbeard [*Crepis* spp.], goldenrod [*Solidago* spp.], and spiders [Araneae]) likely were consumed unintentionally while bears were feeding on other species. Regardless of the exact number of species consumed, the substantial dietary breadth we documented confirms that grizzly bears in the region are opportunistic, generalist omnivores.

Our findings support the notion of Knight et al. (1984) that some diet items were specifically searched out by bears. Knight et al. (1984) referred to this as directed feeding behavior. When available within their home ranges, grizzly bears directed feeding activity toward foods with high gross energy content that could be efficiently foraged, such as army cutworm moths, ungulates, cutthroat trout, clover, small mammals, springbeauty, yampa, whitebark

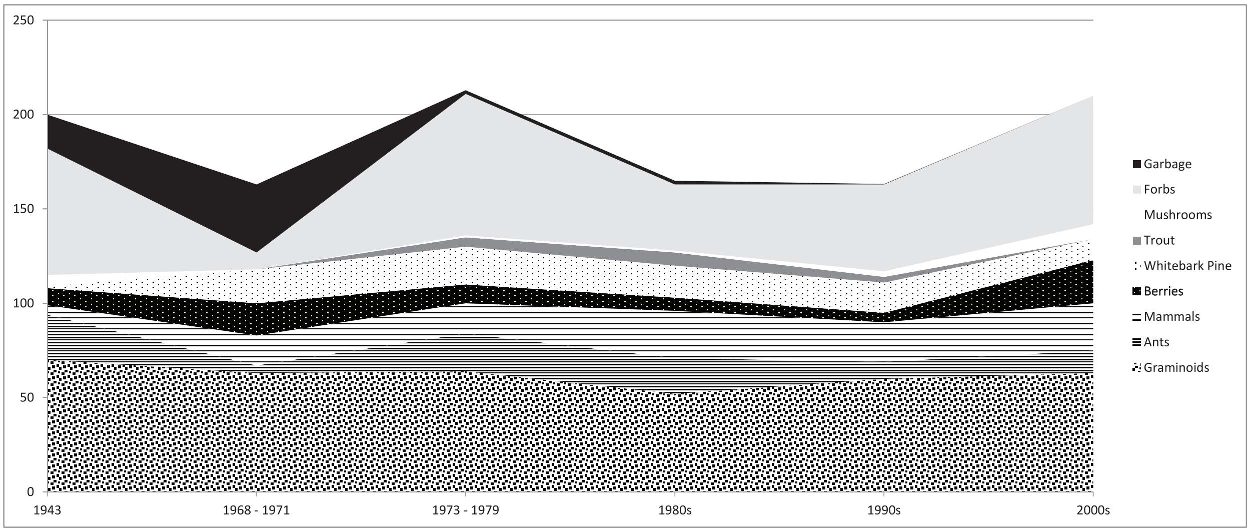

Fig. 1. Percent frequency of occurrence of major food groups detected in grizzly bear scats during different time periods in the Greater Yellowstone Ecosystem, 1943–2009.

pine seeds, biscuitroot, bistort, and horsetail. When these foods were not readily available, bears consumed a wide variety of berries, other forbs, ants, and graminoids. Berries had an average gross caloric value of 3.24 kcal/g (Craighead et al. 1995), but were not consistently available in all parts of the GYE every year (Craighead et al. 1982). Forbs were more consistently available and widely distributed throughout the GYE, but had a lower average gross caloric value (2.88 kcal/g; Craighead et al. 1995) than berries. Ants had relatively low energetic value (2.70 kcal/g; Craighead et al. 1995), but were high in protein (34.3%; Yamazaki et al. 2012) and may also provide essential amino acids that are difficult for bears to obtain from other food items (Eagle and Pelton 1983, Yamazaki et al. 2012). Grasses and sedges had the lowest average gross caloric value (2.52 kcal/g; Craighead et al. 1995), but were the most abundant, widely distributed, consistently available, and consistently consumed grizzly bear food in the GYE. Frequent consumption of graminoids may have been related more to graminoid abundance and distribution than graminoid caloric value or bear preference (Craighead et al. 1982).

Grizzly bears also supplemented their diet with many foods consumed opportunistically, with consumption varying annually based on availability and other factors. Some species were consumed for only a short period each year (e.g., earthworms [Lumbricidae] in meadows at the edge of spring snowmelt), others were available only in small, localized areas (e.g., pondweed [*Potamogeton* spp.] rhizomes from small ephemeral ponds within the Yellowstone caldera), and others such as yellowjackets (*Vespula* spp.), grasshoppers (Orthoptera), and midges (Chironomidae) were consumed primarily during sporadic periods of abundance. Some species were consumed primarily during periods with shortages of more preferred foods (e.g., yellow salsify, fern-leaf licoriceroot), or when opportunistically encountered (e.g., mountain goats [*Oreamnos americanus*], grouse [Phasianidae], boreal chorus frogs [*Pseudacris triseriata maculate*], Utah suckers [*Catostomus ardens*]), likely while foraging for other species. Some diet items of lower caloric value, such as grasses, sedges, and many forbs, may have been consumed in areas between concentrations of higher quality foods, thereby subsidizing travel and search costs (Mattson et al. 1984).

The diversity of foods exploited by GYE grizzly bears is indicative of dietary flexibility, likely enhancing their ability to occupy diverse habitats within the large geographical area that encompasses the GYE. For example, not all high-caloric foods are available to all grizzly bears in the GYE. Cutthroat trout, a high-caloric spring and early summer food (Mealey 1975, Reinhart and Mattson 1990), is not consumed by bears with home ranges outside of the Yellowstone Lake watershed. Haroldson et al. (2005) estimated that only 14–21% of GYE grizzly bears visited Yellowstone Lake spawning streams during 1997–2000. Teisberg et al. (2014) estimated that 8–10% of GYE grizzly bears visited Yellowstone Lake tributary streams during 2007–2009. Grizzly bear feeding activity is highly directed toward bison when available, but bison currently occupy only 1,816 km^2 (<4%; R. Wallen, Yellowstone National Park, personal communication; S. Cain, Grand Teton National Park, personal communication) of the 50,280-km^2 range occupied by grizzly bears (Bjornlie et al. 2014) in the GYE. Therefore, bison are not available to many GYE grizzly bears. Army cutworm moths, a calorically dense food found at high-elevation talus slopes, are highly selected by grizzly bears with home ranges on the east side of the GYE (Mattson et al. 1991b, French et al. 1994). However, most bears on the west side of the ecosystem do not have moth sites within their home ranges and are not known to use this food source. Whitebark pine seeds, another high-elevation food high in calories, are consumed by grizzly bears (Kendall 1983, Mattson et al. 2001). However, within the 50,280-km^2 of occupied grizzly bear range in the GYE (Bjornlie et al. 2014), whitebark pine only occurs on approximately 7,090 km^2 (14%; Interagency Grizzly Bear StudyTeam [IGBST] 2013). Autumn ranges of 29% (n = 72) of grizzly bears monitored with GPS collars in the GYE between 2000 and 2011 did not encompass any mapped whitebark pine habitat, and ranges of another 8 bears (11%) contained <5% whitebark pine habitat (Costello et al. 2014). Of the highest caloric-value foods, elk have the greatest distributional overlap with occupied grizzly bear range in the GYE (Fig. 2). However, even elk may not be available in significant numbers within all GYE grizzly bear home ranges (Fig. 2). Therefore, grizzly bears in the GYE use different food resources depending on where their home ranges are located (Fig. 2). This ecological flexibility has also been reported for other bear populations (Edwards et al. 2011, Van Daele et al. 2012).

Based on scat composition data, one major shift in grizzly bear diets was evident. Consumption of garbage increased from the 1940s through the early 1970s and then declined substantially thereafter. The increase was likely a reflection of increasing numbers of visitors to Yellowstone National Park and the associated availability of garbage. Grizzly bears in YNP had been supplementing native foods with garbage at least since the 1880s (Schullery 1992). From 1968 through 1971, garbage was detected in 36% of grizzly scats and ranked highest in dietary index value for GYE grizzly bears (Craighead et al. 1995). Consumption of garbage declined substantially after municipal garbage dumps were closed during 1968–1979 (Meagher and Phillips 1983, Craighead et al. 1995). Although still occasionally detected in scats from the late 1970s through the late 1980s, garbage was no longer considered a significant diet item during that time (Meagher and Phillips 1983, Mattson et al. 1991a). The most recent food-habits studies conducted in the GYE (Fortin 2011; Podruzny 2012; Orozco and Miles 2013; S. Cain, unpublished data) did not detect garbage as a diet item, although some bears, particularly those outside of the Recovery Zone boundary, still occasionally obtained unsecured garbage (Gunther et al. 2004, 2012).

A second relatively minor diet change involves consumption of Yellowstone Lake cutthroat trout. Although cutthroat trout were reported as a grizzly bear food item early in Yellowstone National Park's history (Jordan 1891, Skinner 1925), early bear use of this food resource was not quantified. Based on the ease with which human anglers caught large numbers of trout in Yellowstone Lake tributaries after the park's establishment in 1872 (Chittenden 1940), cutthroat trout likely were an abundant food for grizzlies (with home ranges around Yellowstone Lake) prior to that time. After establishment of Yellowstone National Park, cutthroat trout in the Yellowstone Lake watershed underwent a long-term period of decline. Commercial fishing, allowed in the park until 1919 to provide food for park hotels (Koel et al. 2005), and liberal recreational fishing regulations from the park's inception through the 1950s, substantially reduced the cutthroat trout population and resulted in a younger and smaller age and size-class structure (Gresswell and Varley 1988). The reduction in trout numbers and size may have made grizzly bear predation on trout energetically inefficient (Reinhart 1990). In bear food-habits studies conducted in 1943 (Murie 1944) and during 1959–1971 (Craighead et al. 1995), trout were not an important diet item. Implementation of increasingly strict fishing regulations beginning in 1969 resulted in cutthroat trout population increase, larger size, and older age structure (Gresswell and Varley 1988), likely increasing the energetic efficiency of trout as a diet item. From the early 1970s through the 1980s, trout were reported as a frequent food item among grizzly bears with home ranges

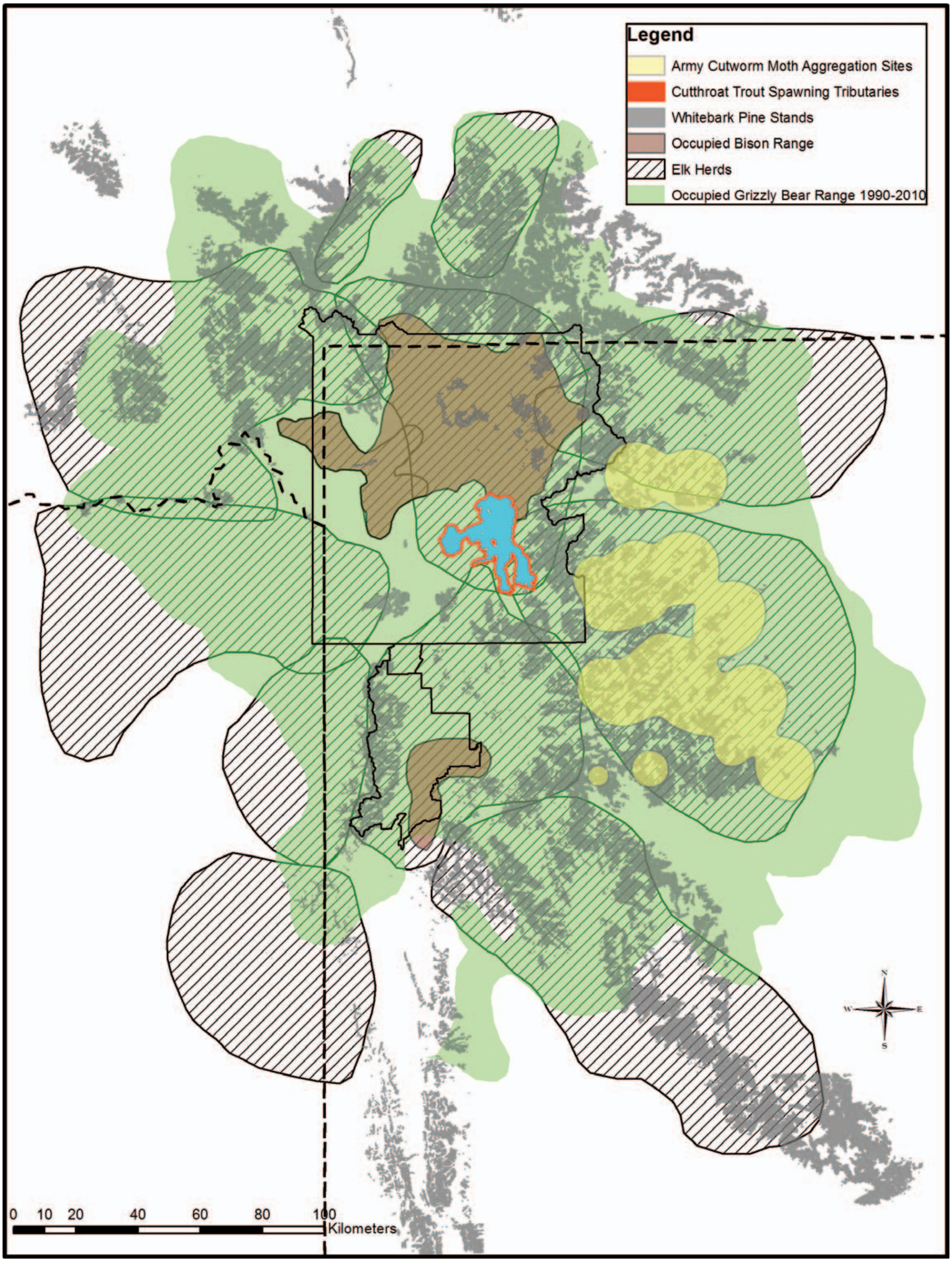

Fig. 2. Distribution of 5 high-caloric grizzly bear foods (army cutworm moths, bison, cutthroat trout, elk, and whitebark pine) within occupied grizzly bear range in the Greater Yellowstone Ecosystem.

adjacent to Yellowstone Lake (Hoskins 1975, Mealey 1975, Reinhart 1990). A second period of decline in both spawning cutthroat trout and bear fishing activity was documented from the early to mid-1990s (Reinhart et al. 1995) and continuing through the late 1990s and the late 2000s (Haroldson et al. 2005, Fortin 2011, Fortin et al. 2013). The introductions of non-native lake trout (*Salvelinus namaycush*) and the exotic parasite (*Myxobolus cerebralis*) that causes whirling disease, combined with a period of drought that reduced juvenile recruitment, were responsible for this second period of decline in cutthroat trout in Yellowstone Lake (Koel et al. 2005, 2006). In the decade between 1997–2000 and 2007–2009, the estimated biomass of cutthroat trout consumed by grizzly bears declined by 70%, and trout were no longer an important diet item for GYE grizzly bears (Fortin 2011, Fortin et al. 2013). Recent studies indicate that grizzly bears with home ranges near Yellowstone Lake have compensated for the current loss of cutthroat trout by preying more heavily on elk calves during spring and early summer (Fortin 2011, Fortin et al. 2013).

The comprehensive nature of our literature review and the longitudinal aspects of the scat data we compiled from previous studies provided unique insights into diet breadth of grizzly bears and broad dietary shifts over time. The diet flexibility demonstrated by Yellowstone grizzly bears likely enhances their ability to occupy diverse habitats over a large geographical area as has been demonstrated in other studies (e.g., Edwards et al. 2011, Van Daele et al. 2012). This diet flexibility likely also enhances their ability to cope with short- and long-term perturbations in the abundance of preferred, high-caloric foods. The list of grizzly bear diet items we compiled will help managers of grizzly bears and their habitat document changes in foods consumed. This information will help managers increase their understanding of how bears may respond to changing food resources, providing them with a strong foundation for making decisions about future grizzly bear management in the GYE (Schwartz et al. 2013).

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Supplemental material

Table S1. Diet items detected through direct observation of feeding activity, feeding-site examination, or scat analysis, consumed by grizzly bears in the Greater Yellowstone Ecosystem from 1891 to 2013.

Table S2. Reported nutritive and caloric values of grizzly bear foods in the Greater Yellowstone Ecosystem.

Literature cited for Tables S1 and S2.